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THE EFFECTS OF ACROBATIC TRAINING ON THE PERFORMANCE OF TASKS REQUIRING SKILLED MOTOR PERFORMANCE

BY

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TABLE OF CONTENTS

ABSTRACT

Black et. al. (1990) examined the role of the cerebellar cortex in motor learning in rats. They used four experimental conditions: an acrobatic (learning) condition, a forced exercise condition, a volunteer exercise condition, and an inactive condition. When the cerebellar cortex was studied, Black et al. (1990) found that rats in the acrobatic condition had more synapses per Purkinje cell in the paramedian lobule than any of the other three groups. There were no significant differences among the inactive group and the exercise groups (non-learning). This seemed to indicate that learning, rather than activity, was associated with the synaptogenesis. The purpose of the current experiment was to investigate more thoroughly the idea presented by Black et. al. (1990) that motor learning occurs during acrobatic training. In the current experiment, acrobatically trained, volunteer exercise, and inactive rats were tested on a rotating rod and a rope apparatus. Three criteria for learning were explored in the current study: the increased proficiency of performing the acrobatic training tasks over time, the performance of new test tasks, and the persistence of the acquired skill over time. Rats became more proficient at performing the acrobatic tasks over the training period. Also, rats in the learning condition performed better than those in the non-learning condition on the first day of the new test tasks. Finally, rats that had a

delay between training and testing performed at least as well as those tested immediately on the test tasks. Overall this investigation supported the idea that learning occurred in the acrobatic condition.

In 1990, Black, Isaacs, Anderson, Alcantara, and Greenough examined the role of the cerebellar cortex in motor learning. They looked for anatomical plasticity in the cerebellar cortex that was associated with motor learning. They used four experimental conditions in which the rats were caged individually. The first group of rats was trained on a series of obstacles requiring motor coordination, particularly skilled movements and balance. Over the trials the rats improved in their ability to traverse the course of obstacles in a skilled manner. The second condition involved forced exercise on a treadmill. The rats mastered the treadmill by the first day of use, which indicated that very little learning was needed to perform this task. The third group had a running wheel attached to each cage and was referred to as the "volunteer exercise" group. Within three days, the volunteer exercise rats mastered the balancing and coordination required to use the running wheel. The final group of rats had minimal opportunities for learning or exercise and were thus called "inactive."

When the cerebellar cortex was studied, Black et al. (1990) found that rats in the acrobatic condition had more synapses per Purkinje cell in the paramedian lobule than rats in any of the other three groups. There were no significant differences among the inactive group and the exercise groups. However, the blood vessel density in the paramedian lobule of

the rats in the exercise conditions was significantly higher than either the inactive condition or the acrobatic condition. The increased blood vessel density was evidence that the paramedian lobule is metabolically active during exercise. These two observations seemed to indicate that learning caused synaptogenesis on the Purkinje cells and that the neural activation of the synapses caused by the exercise is not sufficient to cause the formation of new synapses.

The learning curve provided in Black et. al. (1990) showed that the average amount of time to perform an acrobatic task decreased over the days of training. This was not sufficient evidence to conclude definitively that the acrobatic paradigm involves motor learning. Problems changed across days, and the completion times were not measured by an automatic system. Moreover, if the number of errors per task demonstrated a typical negatively decelerated acquisition curve, it would help establish acrobatic training as a learning paradigm. Several criteria need to be satisfied to establish that learning is required for successful performance of the acrobatic obstacles. Therefore, the purpose of this study was to assess the evidence that learning is involved in the competent execution of the acrobatic tasks. This was achieved by systematically observing and recording the daily performance of the rats on the acrobatic tasks (i.e. a learning curve), and by demonstrating that other criteria of learning are satisfied by this paradigm.

Two additional characteristics of learning were addressed by the present study, the generalization of knowledge to similar tasks and the maintenance of memory over a period of time.

There are several other experiments in which neuronal morphological changes have been associated with learning. Beginning in the 1940's, D.O. Hebb revolutionized the way neural memory was conceptualized in animals. He determined that there was an approachable way to test the association between psychology and physiology, and that this would enhance the understanding of the relationship between the brain and behavior. Hebb suggested that an experimenter should manipulate the experience of an animal, and then check the subsequent behaviors and changes in the brain that would correspond to memory. An extensive body of research has resulted from this general design for studying information storage.

Environmental manipulation paradigms were created as direct consequences of Hebb's philosophy. Behavioral studies showed that exposing a rat to a complex environment as opposed to an isolated or social environment, improves its performance on complex motor tasks and mazes (Bingham & Griffiths, 1952; Brown, 1968; Greenough, Fulcher, Yuwiler, & Geller, 1970; Hebb, 1949).

Anatomical studies determined that structural changes in the brain underlie the learning demonstrated in the animals

exposed to a complex environment. For example, the cerebral cortex of rats exposed to a complex environment is heavier and thicker than the cerebral cortex of rats in either social or isolated environments (Bennett, Diamond, Krech, & Rosenzweig, 1964). Several kinds of cellular changes seem to underlie this change in gross morphology. The changes in cortex observed in rats with complex experience are most prominent in the visual cortex. Rats with enriched experience had more dendrites and synapses per neuron in their visual cortex than the isolated rats (Greenough, Withers, & Wallace, 1990; Turner & Greenough, 1984; Volkmar & Greenough, 1972).

Some experimenters suggested that the cellular alterations demonstrated in the brains of animals exposed to complex environments could be due to non-specific changes in metabolism and hormone secretion rather than learning in these animals. These nonspecific possibilities were tested by Chang and Greenough (1982). These authors showed that split-brain rats trained in unilateral paradigms demonstrated differences in the dendritic branching of the pyramidal cells in the visual cortex of the hemisphere corresponding to training. In addition, it has been demonstrated that the brain changes in the complex environment occurred in areas specifically using the learned information (Chang & Greenough, 1982; Greenough, Juraska, & Volkmar, 1979; Greenough, Larson, & Withers, 1985).

Some researchers have proposed that rats in the isolated

condition might be chronically stressed. The brain damage caused by chronic stress could decrease the number of dendrites and synapses per neuron, which would suggest an apparent increase in animals exposed to the complex environment. However, Black, Sirevaag, Wallace, Savin, and Greenough (1989) found that the while there was considerable variability in the adrenal weights of the rats, this variability was not related to housing condition. This demonstrated that the isolated rats were no more or less stressed than the rats in other conditions. Other evidence that the changes found in the brains of complex environment rats are a form of memory is that the increased dendritic branching found in the occipital cortex persists beyond the experience of living in the complex environment (Camel, Withers, & Greenough, 1986).

In addition to the cerebral cortex, the cerebellum has been implicated as a location of learning (Albus, 1971; Black et al., 1990; Eccles, 1977; Ito, 1984; Lalonde & Botez, 1990; Marr, 1969). Albus (1971) and Marr (1969) used associative learning models to argue that the cerebellum was a pattern recognition data processing system that stored its memory in the Purkinje cells of the cerebellar cortex. Eccles (1977) suggested that the cerebellum is more complex than was intimated by the models originally suggested by Albus and Marr. In particular, he argued that the conjunction of climbing fiber and mossy fiber activity in the cerebellar cortex are involved

in cerebellar modification. In either case, the anatomy of the cerebellum indicates it would be an ideal location for learning, based on the modification of selected synapses.

We have seen that there are changes associated with learning found in the cerebral cortex as a function of environmental manipulations. Studies have also found that there are alterations in the cerebellar neuronal morphology associated with environmental manipulations (Floeter & Greenough, 1979; Greenough, McDonald, Parnisari, & Camel, 1986; Pysh & Weiss, 1979). Floeter and Greenough (1979) reared monkeys in three conditions. The first condition was an isolated environment with very limited sensory and motor availability. Another condition, the social condition, involved housing pairs of monkeys in adjacent cages and allowing them to interact with each other for several hours every day. The final condition was the colony condition in which the monkeys were housed in a semi-naturalistic setting. Floeter and Greenough found that the monkeys reared in the colony had an increase in the size of the spiny branchlets and in the somas of the Purkinje cells, which are located in the cerebellar cortex.

Pysh and Weiss (1979) reared mice in one of two separate conditions. The physically active mice were raised in a large cage which contained a variety of exercise equipment, and each active mouse was trained on a variety of complex motor tasks.

On the other hand, mice in the inactive condition were raised together in a small cage where movement was restricted. The active group's Purkinje cells had larger dendritic trees and more spiny branchlets than the cells from the inactive mice. These studies were the first to indicate that there is structural plasticity in the cerebellar cortex of developing animals.

The discovery of plasticity in the cerebellar cortex of young animals lead to research examining the cerebellar cortex of old adult animals. In 1986, Greenough, McDonald, Parnisari, and Camel studied the cerebellum of adult rats exposed to a complex environment. They found significantly more spiny branchlets on the dendrites of the Purkinje cells of the rats that were exposed to the enriched environment as opposed to rats housed in standard laboratory cages. Greenough et al. (1986) proposed that the increased number of spiny branchlets was induced by the enhanced sensory-motor learning in the complex environment.

Beyond the histological studies of the cerebellum, Gilbert and Thach (1977) performed an experiment in which Purkinje cell activity was recorded during motor learning. During learning, the Purkinje cells emit complex spikes whereas, when the learning is complete the Purkinje cells fire predominantly simple spikes (Gilbert & Thach, 1977). Modifications in the strength of the parallel fiber synapses on the Purkinje cells

are believed to be involved in learning and the firing of the parallel fibers controls the firing of the Purkinje cells. Therefore this change in Purkinje cell transmission supports the idea that motor learning is associated with changes in the cerebellum.

Other learning paradigms have also implicated cerebellar involvement in learning. The memory circuit for the acquisition of the classically conditioned nictitating membrane response has been extensively studied (Turker & Miles, 1986; reviewed in Lalonde & Botez, 1990; Thompson, 1986; Thompson, 1989). The paradigm consists of a corneal air puff or a periorbital electric shock as the unconditioned stimulus that is paired with a light or a tone (conditioned stimulus) until the conditioned stimulus alone elicits the blink of the animal's eyelid (conditioned response). Lesions to the various parts of the cerebellar deep nuclei and cerebellar cortex impair or abolish the conditioned response. The cerebellum also appears to be involved in acquisition of habituation of the acoustic startle response (reviewed in Ito, 1984; Lalonde & Botez, 1990). This paradigm involves exposing an animal to a series of loud tones in order to elicit a startle response until the animal's response decreases substantially across trials. Lesions in any part of the primary circuit pathway of this memory circuit destroy the ability of the animal to habituate (Lalonde & Botez, 1990).

Certain changes in the vestibulo-ocular reflex demonstrate another example of the cerebellum's involvement with associative motor learning (reviewed in Ito, 1984; Thompson, 1986). The vestibulo-ocular reflex holds the images of the world stationary across the retina during head movements. Adaptation of the vestibulo-ocular reflex has been observed when lenses that change the visual field of the animal are placed over their eyes. This adaptation can be seen behaviorally. Beyond this, lesions to the memory circuit pathway can abolish the vestibulo-ocular reflex adaptation (Ito, 1984; Thompson, 1986). Overall these simple motor learning paradigms (eyelid conditioning, startle habituation, and vestibulo-ocular reflex adaptation) seem to indicate that learning occurs in the cerebellum.

The study to be described in this paper used the protocol for acrobatic training described in Black et. al. (1990) to further explore the idea that the acrobatic training yields learning. The behavior of the animals was examined in more detail to determine if they show the "classic" learning curve on the acrobatic tasks. Learning curves were generated using data from both time to complete the task and number of errors per task. Unlike the Black et. al. (1990) study, time per obstacle data was generated from automated timing devices. The generalization of knowledge to novel tasks, requiring skilled motor performance was tested by placing the rats on a rotating

rod apparatus and on a vertical rope to climb. This generalization was tested because part of learning is the ability to apply previously learned knowledge to a new task.

The choice of the rotating rod as a general motor task was based on the fact that a functioning cerebellum has been implicated as necessary for traversing a similar rod (Pellegrino & Altman, 1979). In this study, infant rats were X-irradiated at different levels which caused different amounts of damage to cerebellar cortex. The rats were tested on their ability to cross various rods. There were five variables that could be manipulated to increase or decrease the difficulty of the task. The most basic variable was the diameter of the rod. The thinner the rod was the more difficult it was for a rat to keep its balance and cross it. Another variable was whether the rod was smooth or rough. The rough rods were rolled in sand while the paint on them was still wet. The rat had more traction and found it easier to cross a rod if it was rough. The next variable was the size of the hurdles placed on the rod. The smaller hurdles were easier for a rat to climb over. More than one height of hurdle could be used on the same rod. In this case a rod with hurdles of varying heights was more difficult for a rat to cross than a rod with hurdles of constant height. The final variable was whether or not the rod was rotating. If the rod was rotating the rat had to learn to compensate for the lateral displacement of its body while

trying to overcome any other obstacles it encountered while crossing the rod. The rod's speed of rotation also affected the rats performance. When the rod rotated at faster speeds the rat fell off the rod with a greater frequency than when the rod was rotating at slower speeds. Presumably, practice at any level of this task of traversing a rod would improve the skill with which the rat performs it. Irradiated rats were slower and fell off the rods more often than controls, which seems to imply that an intact cerebellum is necessary to traverse the rod (Brunner & Altman, 1971; Pellegrino & Altman, 1971).

In Altman, Anderson, and Strop (1971), X-irradiated rats were tested in their ability to climb a vertical rod and cling to a rope. Rats with intact cerebellums performed more proficiently than controls. For the current experiment these two task were combined to develop a rope climbing task.

If the number of errors per acrobatic task decreases with increasing exposure to the task, and the amount of time per task also decreases, then learning is required. Given that learning should generalize to similar tasks, the acrobatically trained rats should be more proficient at traversing the rod and climbing the rope than either the rats in the inactive condition or the volunteer exercise condition. If, according to the criteria mentioned above, the data indicate that acrobatic training involves learning, then we can assume that the cerebellar effects reported by Black et. al. (1990) are

associated with learning. Learning should also persist. If some rats are placed in isolation for a thirty day period after training and before motor skills testing, they should demonstrate the retention of the motor memory developed by the acrobatic training over a period of time.

METHODS

Subjects

Laboratory bred female Long-Evans hooded rats were used for this investigation. A total of 26 females from three litters were trained in various conditions for the experiment. Three rats, one in the acrobatic condition and two in the inactive condition, contracted an unidentified disease. Although these rats participated in all aspects of the experiment, their data were not included in the data analysis. The rats were approximately 75 days old at the start of the experiment. They were maintained with a 12:12 reverse light-dark schedule and the room temperature ranged from 70-74° Fahrenheit. Food and water were available ad lib until 24 hours before testing began. All rats were weighed and placed in separate cages on the first day of the experiment.

Procedure

Each rat participated in one of three 25 day training conditions and either immediate or delayed testing (see Table 1). During training, the rats were weighed weekly. Littermates were assigned randomly, but evenly across all training groups.

Training

Acrobatic Condition

Ten female rats were individually caged in standard cages. These rats were trained for 25 days on an elevated path of an

increasingly difficult series of acrobatic motor tasks. The obstacles included suspended dowels, balance beams of various widths, a see-saw, ropes and ladders placed horizontally, and a swinging bridge (see Figure 1). Verbal encouragement by the investigator, combined with squeezes of the hindquarters, served as effective motivation when needed for the rat to traverse the obstacle course. The mean number of errors per task was calculated by dividing the total number of errors committed during the trial by the number of tasks. Some of the errors that were observed were foot faults, slips, slips under, turns, twists, and falls. A foot fault involved the paw of the rat not precisely moving to the next position on the obstacle. A slip was a more severe mistake and involved the rat placing its paw into the air next to the task rather than on the equipment. When the rat slipped under the equipment, it hung on the apparatus in an upside down position until a researcher placed it back on the equipment correctly. Another error was when a rat would turn around and try to either avoid a task or traverse the previously crossed tasks backwards. A twist involved a rat's body twisting off the apparatus while the rat's paws remained on it. Finally, a rat fell when the whole rat fell off of the equipment. All errors were interruptions in the smooth performance of the tasks. Similar to the errors, the total time for a trial was divided by the number of tasks on that trial to calculate the mean amount of

time the rat took to traverse a single task. The area below the obstacle course was covered in rubber foam, such that, if a rat fell off, it would not be injured.

Volunteer Exercise Condition

Ten rats were housed individually in standard cages that were attached to running wheels (see Figure 2). The rats had free access to these 36 cm diam × 14 cm wide wheels. Wheel rotations were monitored and the rats were handled for several minutes daily. This condition provided extensive motor activity without extensive learning on the rat's performance of the test motor tasks.

Inactive Condition

The remaining six rats were housed individually in standard cages where they had very little opportunity for motor activity and learning (see Figure 2). The rats were handled for several minutes daily.

Testing

Half of the rats from each training condition were tested immediately and the other half were inactive for thirty days. The testing period was 4 days (see Table 2). For the rats for which testing was delayed, food and water were available ad lib until 24 hours before testing, they were weighed weekly and handled daily.

Food Deprivation

In order to create a motivation for the motor tasks during testing, a food deprivation schedule was implemented, and a reward was provided for completing the task. The reward consisted of a quarter of one Froot Loop. The rats were given one Froot Loop per day for two weeks prior to testing, while in their cages to familiarize them to this novel food. Twenty-four hours prior to testing, each rat was weighed and the ad lib food supply was replaced with 12g of food. The rats were fed 12g of food per day for the duration of testing. Water continued to be available ad lib.

Rotating Rod

Equipment. The rotating rod apparatus consisted of a 7 ft x 2 ft x 2.5 ft plywood box containing a 4 inch diameter PVC tube suspended 2 feet above the bottom. Each rod was a 6 foot long painted piece of PVC tube. To roughen the rough rod, it was rolled in sand while the paint was wet. The hurdles consisted of one inch diameter foam strips wrapped around and connected to the rod every 12 inches. The rod was connected to a Bodine NSH-34RH gearmotor which created the rotation. A 24 x 6 inch start platform was located above the rod on the side of the rod closest to the motor and a same sized goal platform was located on the other end of the rod. Foam was placed throughout the bottom of the box in order to prevent injury in the event of a fall.

Procedure. Each day of testing every rat crossed the rotating rod three times at each of four speeds (see Figure 3). On the first, second, and third days the rats ran across a rod that was rotating at 0 rpm, 6 rpm, 15 rpm, and 25 rpm. On the fourth day, the rotation speeds were 0 rpm, 10.5 rpm, 20 rpm, and 27.3 rpm. Three different rods were used. The rods were changed daily until the third day. The first rod was a smooth rod with no hurdles. A rough rod with hurdles was used on the second day. On the third and fourth days, a smooth rod with hurdles was used. All trials were observed by two people and notes were taken on the quality of performance and the amount of time used to cross the rod. If a rat took longer than four minutes to cross the rod, then the trial was considered to take four minutes.

Rope Climbing

Equipment. A vertical piece of rope was strung between a wooden base and a wooden platform 24 inches from the base.

Procedure. After trials on the rotating rod, the rats were placed on the vertical rope apparatus. On each day of testing every rat climbed the rope three times (see Figure 3). On the first day, the rats climbed a 3/4" diameter rope. A 1/2" diameter rope was used on the second day, and a 1/4" diameter rope was used on both the third and the fourth days of testing. A 1/4 of a Froot Loop was placed on the elevated platform as incentive for the rat to climb the rope. All

trials were observed by two people and notes were taken on the quality of performance and the amount of time used to climb the rope. If a rat took longer than two minutes to climb the rope, then the trial was considered to take two minutes.

RESULTS

The purpose of this experiment was to more thoroughly investigate the idea presented by Black et. al. (1990) that motor learning occurs during acrobatic training. Three criteria for learning were explored by the current study: the increased proficiency of performing similar tasks over time (acquisition curve), the manipulation and application of knowledge gained from an initial learning experience in the performance of new tasks (generalization test), and the persistence of the acquired skill over time (memory test).

Acquisition Curve

To determine whether learning occurred over the process of acrobatic training, the average number of errors per task and amount of time on the acrobatic equipment was calculated (see Figures 4 and 5). The number of errors per task were averaged over five day intervals. A one way analysis of variance of the five day intervals showed that the rats made significantly fewer errors per task during the last ten days of training than during the first fifteen days ($F(4,45) = 8.60$, $p<.01$). The first three intervals were significantly different from the fourth and fifth intervals according to the Student Newman Keuls test. The average time per task did not seem to improve over the duration of the training period. When time was averaged across five day intervals, there was no significant difference among the intervals as far as average amount of time

taken to perform the complex motor tasks was concerned. Thus, the trend in errors (but not in time) demonstrated that the rats became more proficient at performing complex motor tasks.

Since several animals became sick and unusable for the experiment, the number of inactive condition rats was severely diminished. In order to compensate for the small number of inactive condition rats, these rats were combined with the volunteer exercise condition rats to create the non-learning condition. The acrobatic training condition rats were designated the learning condition.

Generalization Test

The generalization of knowledge gained from one set of tasks to another set of tasks was examined by comparing times and error data on the rotating rod from learning and non-learning groups, averaged over immediate and delayed conditions. Both number of errors committed and amount of time taken by the rat to cross the rod apparatus were determined. A repeated measures analysis of variance was run on the data. All measures showed that the performance of the rats across the days of testing was significantly different. In fact, on both the rod and the rope, there was a day by group interaction ($F(3,17) = 4.78$, $p<.05$, $F(3,17) = 9.90$, $p<.05$, respectively). Although there were no significant group differences when the data for all of the days were combined, there were significant differences on the first day. The learning group had

significantly fewer errors ($F(1,19) = 5.99$, $p<.05$) and used significantly less time to cross the rod apparatus ($F(1,19) = 6.14$, $p<.05$.) than the non-learning group (see Figures 6 and 7). Also on the first day, the learning condition rats climbed the rope apparatus faster than the non-learning rats ($F(1,19) = 24.90$, $p<.05$)(see Figure 8). On the rope apparatus, only the time taken to climb up could be assessed accurately. The number of errors the rat made while climbing the rope was difficult to observe. The differences between the groups were not significant for days two, three, and four of the testing.

Memory Test

The performance of the immediately tested rats was compared to the rats that were inactive for thirty days (delay), averaged over learning and non-learning groups. The immediately tested group made significantly more errors on the first day on the rotating rod than the delayed group ($F(1,19) = 8.44$, $p<.05$)(see Figure 9). Also, on the third day, the immediately tested rats took more time to climb the rope than the delayed group ($F(1,19) = 4.74$, $p<.05$)(see Figure 10). For amount of time taken to cross the rod, there was no significant difference between the immediate and delayed groups (see Figure 11). These results are contrary to those expected, because the rats that were inactive for 30 days were either significantly more proficient at the selected tasks or they were not significantly different.

A significant interaction between the learning factor and the delay factor on the first day times on the rod was also found ($F(1,19) = 4.65$, $p<0.05$). The delayed non-learning group took much longer ($\bar{X} = 47.4$, s.d. = 23.2) to cross the rod than the immediate learning ($\bar{X} = 24.9$, s.d. = 20.9), immediate non-learning ($\bar{X} = 26.9$, s.d. = 7.2), and delayed learning groups ($\bar{X} = 18.5$, s.d. = 1.0). The non-learning groups were affected by the delay whereas the learning groups were not. This interaction was also significant for both the first and second days on the rope ($F(1,19) = 9.96$, $p<0.05$, $F(1,19) = 7.95$, $p<.05$). Similar to the rod interaction, on the first day, the delayed non-learning group took longer ($\bar{X} = 94.7$, s.d. = 33.3) to climb the rope than the other three groups ($\bar{X}$(immediate, learning) = 33.0, s.d. = 19.3, $\bar{X}$(immediate, non-learning) = 51.9, s.d. = 23.0, $\bar{X}$(delayed, learning) = 10.5, s.d. = 5.4). However, on day two, the learning groups were affected by the delay ($\bar{X}$(immediate) = 69.8, s.d. = 45.8, $\bar{X}$(delayed) = 15.9, s.d. = 1.8), and non-learning groups were not ($\bar{X}$(immediate) = 38.0, s.d. = 20.5, $\bar{X}$(delayed) = 58.7, s.d. = 39.1). This interaction indicated that the learning and the non-learning groups reacted differently to immediate and delayed testing.

DISCUSSION

The data collected in this study provided evidence both supporting and not directly supporting the hypothesis that acrobatic training is a form of learning. Although the mean number of errors per acrobatic task increased when certain new tasks were added to the acrobatic path, the overall trend was for the mean number of errors per task to decrease. On the other hand, the average time per task did not decrease. This lack of a completion time decrease could be due to several factors. First, some rats performed the tasks accurately, but slowly. There was no incentive for speed over accuracy. Second, some rats stopped on the platforms before particular tasks that were either new or that they had trouble performing on a previous trial. Third, as the 25 days progressed, more difficult tasks were added to the course, perhaps requiring slow and careful performance or inducing more pausing on platforms. Another reason for an irregular pattern of mean times may be that the amount of time taken to perform a task is related to the rat's estrous cycle (Anderson, in progress).

The average time per task reported in this study was very different than that in the original study (Black et. al., 1990). In Black et. al. (1990), the mean times per task approximately ranged from 2½ minutes to 30 seconds, whereas the in the current study the mean times ranged from 14½ seconds to 11 seconds. The longest time in the current study was less

than the shortest time measured in the Black et. al. (1990) study. This difference may be accounted for in two ways. First, the current study used younger rats, which seem to be able to learn faster. In support of this, it has recently been found that 12 month old rats show a negatively decelerated acquisition curve for time per acrobatic task across the training period (Haglund, in progress). This demonstrates that older rats apparently have a more difficult time adapting to performing the acrobatic motor tasks, and are most likely learning more. Older rats in non-learning conditions may also have more difficulty learning test tasks than the younger rats used in the current experiment. Therefore, in older rats, time in addition to number of errors per task could be used as indicators demonstrating the effects of the acrobatic training on the test tasks. Also, the experimenters were more proficient at running the rats on the acrobatic equipment in this experiment than when the original study was executed.

Overall, the learning group rats performed better on the rotating rod and the rope apparatus on the first day of testing. During the next three days there were no significant differences between the learning and the non-learning groups. Over the test period both the learning and non-learning groups rapidly learned how to perform the tasks more proficiently. Both groups of rats were fastest when traversing the rough rod with hurdles, while the smooth rod with hurdles seemed to be

the most difficult to traverse. In addition, when the speeds of rod rotation for each trial were increased on the fourth day of testing, both the learning and the non-learning groups made more errors. On the rope apparatus, the two groups climbed at very similar speeds on the second, third, and fourth day of testing. Both groups improved their climbing time at approximately the same rate over the last three days of testing. All of these observations indicate that beyond the first day of testing the rate of learning is unaffected by training condition. This consistency of results across tasks argues that no differences were seen between the learning and non-learning groups beyond the first day because the rats could master the tasks quickly, which is possibly because the rats were young. Another possibility is that the tasks were easy to learn and harder tasks would have shown differences in the performance of the groups beyond the first day.

For the most part, the rats that were tested immediately performed worse on the testing apparatus than the rats that were inactively detained for thirty days. One explanation could be that the rats from the acrobatic condition were experiencing interference. In addition, the volunteer exercise rats were particularly difficult to handle immediately after being removed from their cages with the running wheels attached. Also, the experimenters were more experienced with the testing procedures when the rats that were tested after the

30 day delay. Because the delayed animals either performed better or were not significantly different from the immediately tested animals, the learning experienced by the rats did seem to persist over the inactive delay.

Further experiments could compare the immediate group to the delayed group anatomically. This would address the possible anatomical persistence of the structural changes in the paramedian lobule of the cerebellum associated with acrobatic training. Also, this identical experiment could be run with older animals, so that it could be directly compared with Black et. al. (1990). More distinct differences in the performances of the groups might be seen with a larger or older population of animals.

Overall, this investigation supported the idea that learning occurs during acrobatic training. The rats became more proficient at traversing the acrobatic path over the 25 day training period, which was shown by their decrease in mean errors per task. The rats in the learning group performed the test tasks more accurately and faster on the first day of testing, which indicated that the rats generalized their acrobatic training skills to their performance on the rotating rod and the rope apparatus. The rats in the delayed group performed at least as well as the rats that were immediately tested which suggested that the learning that occurred as a result of acrobatic training persisted for the 30 day period.

Because the volunteer exercise rats have a different experience than the inactive rats, future experiments should investigate possible differences between their performances on the rotating rod and rope apparatuses. Volunteer exercise rats were difficult to handle when they were removed from their cages that were attached to running wheels, however they settled down after they had been in the standard cages for one day. Also, an experiment where the amount of delay between training and testing is varied would help establish the time course of the persistence of acrobatic training effects. If the time courses observed for the development and decay of the effects of acrobatic training are similar to the development and decay of structural changes observed in the paramedian lobule of the cerebellum, then this structural change would be considered a likely component of the anatomical substrate for motor learning.

REFERENCES

Albus, J. S. (1971). A theory of cerebellar function. Mathematical Biosciences, 10, 25-61.

Altman, J., Anderson, W. J., & Strop, M. (1971). Retardation of cerebellar and motor development by focal x-irradiation during infancy. Physiology and Behavior, 7, 143-150.

Bennett, E. L., Diamond, M. C., Krech, D., & Rosenzweig, M. R. (1964). Chemical and anatomical plasticity in the brain. Science, 146, 610-619.

Bingham, W.E., & Griffiths, W. J., Jr. (1952). The effect of different environments during infancy on adult behavior in the rat. Journal of Comparative and Physiological Psychology, 45, 307-312.

Black, J. E., Isaacs, K. R., Anderson, B. J., Alcantara, A. A., & Greenough, W.T. (1990). Learning causes synaptogenesis, whereas motor activity causes angiogenesis, in the cerebellar cortex of adult rats. Proceedings of National Academy of Sciences, USA, 87, 5568-5572.

Black, J. E., Sirevaag, A. M., Wallace, C. S., Savin, M. H., & Greenough, W. T. (1989). Effects of complex experience on somatic growth and organ development in rats. Developmental Psychobiology, 22, 727-752.

Brown, R. T. (1968). Early experience and problem solving-ability. Journal of Comparative and Physiological Psychology, 65, 433-440.

Brunner, R. L., & Altman, J. (1973). Locomotor deficits in adults rats with moderate to massive retardation of cerebellar development during infancy. Behavioral Biology, 9, 169-188.

Camel, J. E., Withers, G. S., & Greenough, W. T. (1986). Persistence of visual cortex dendritic alterations induced by postweaning exposure to a "superenriched" environment in rats. Behavioral Neuroscience, 100, 810-813.

Chang, F. F., & Greenough, W. T., (1982). Lateralized effects of monocular training on dendritic branching in adult split-brained rats. Brain Research, 232, 283-292.

Eccles, J. C. (1977). An instruction selection theory of learning in the cerebellar cortex. Brain Research, 127, 327-352.

Floeter, M. K., & Greenough, W. T. (1979). Cerebellar Plasticity: Modification of Purkinje cell structure by differential rearing in monkeys. Science, 206, 227-229.

Gilbert, P. F. C., & Thach, W. T. (1977). Purkinje cell activity during motor learning. Brain Research, 128, 309-328.

Greenough, W. T., Fulcher, J. K., Yuwiler, A., Geller, E. (1970). Enriched rearing and cnronic electric shock: effects on brain behavior in mice. Physiology and Behavior, 5, 371-373.

Greenough, W. T., Juraska, J. M., & Volkmar, F. R. (1979). Maze training effects on dendritic branching in occipital cortex of adult rats. Behavioral and Neural Biology, 26, 287-297.

Greenough, W. T., Larson, J., & Withers, G. (1985). Effects of unilateral and bilateral training in a reaching task on dendritic branching of neurons in the rat motor-sensory forelimb cortex. Behavioral and Neural Biology, 44, 301-314.

Greenough, W. T., McDonald, J. W., Parnisari, R. M., & Camel, J. E. (1986). Environmental conditions modulate degeneration and new dendrite growth in cerebellum of senescent rats. Brain Research, 380, 136-143.

Greenough, W. T., Withers, G. S., & Wallace, C. S. (1990). Morphological changes in the nervous system arising from behavioral experience: What is the evidence that they are involved in learning and memory?. In L. R. Squire & E. Lindenlaub (Eds.), The Biology of Memory (pp. 159-185). New York: F.K. Schattauer Verlag.

Hebb, D. O. (1949). The Organization of Behavior. New York: John Wiley & Sons.

Ito, M. (1984). The Cerebellum and Neural Control. New York: Raven Press.

Lalonde, R., & Botez, M.I. (1990). The cerebellum and learning processes in animals. Brain Research Reviews, 15, 325-332.

Marr, D. (1969). A theory of cerebellar cortex. The Journal of Physiology, 202, 437-470.

Pellegrino, L. J., & Altman, J. (1979). Effects of differential interference with postnatal cerebellar neurogenesis on motor performance, activity level, and maze learning of rats: A developmental study. Journal of Comparative and Physiological Psychology, 93, 1-32.

Pysh, J. J., & Weiss, G. M. (1979). Exercise during development induces an increase in Purkinje cell dendritic tree size. Science, 206, 230-231.

Thompson, R. F. (1986). The neurobiology of learning and memory. Science, 233, 941-947.

Thompson, R. F. (1989). Neural circuit for classical conditioning of the eyelid closure response. In J. H. Byrne & W. D. Berry (Eds.). From Neural Models of Plasticity: Experimental and Theoretical Approaches (pp. 160-177). San Diego: Academic Press.

Turker, K. S., & Miles, T. S. (1986). Climbing fiber lesions disrupt conditioning of the nictitating membrane response in the rabbit. Brain Research, 363, 376-378.

Turner, A. M., & Greenough, W. T. (1985). Differential rearing effects on rat visual cortex synapses. I. Synaptic and neuronal density and synapses per neuron. Brain Research, 329, 195-203.

Volkmar, F. R., & Greenough, W. T. (1972). Rearing complexity affects branching of dendrites in the visual cortex of the rat. Science, 176, 1445-1447.

TABLE 1 Experimental Design

	Training Condition		
Testing Condition	**Acrobatic Training**	**Volunteer Exercise Condition**	**Inactive Condition**
Immediate	n = 4	n = 5	n = 2
Delay	n = 5	n = 5	n = 2

TABLE 2 Testing Schedule

	DAY 1	DAY 2	DAY 3	DAY 4
ROD	smooth	rough	smooth	smooth
Hurdles	no	yes	yes	yes
RPM	0, 6, 15, 24	0, 6, 15, 24	0, 6, 15, 24	0, 10.5, 20, 27.3
ROPE	3/4"	1/2"	1/4"	1/4"

FIGURE CAPTIONS

Figure 1. Acrobatic condition (learning) rat climbing down a ladder, crossing a spring bridge, and walking over a seesaw during acrobatic training. These were some of the tasks used as complex motor tasks for the motor learning paradigm.

Figure 2. Volunteer exercise rat running in the running wheel attached to its cage. Inactive condition rats in their standard cages. These two groups were combined to create the non-learning group.

Figure 3. Rat traversing the smooth rotating rod with hurdles. Rat climbing the 1/4" diameter rope on the rope apparatus.

Figure 4. Mean number of errors made on each acrobatic task averaged across five day intervals. Letters indicate that during the last ten days (b) the rats made significantly fewer errors than during the first fifteen days (a), $p < .05$.

Figure 5. Mean amount of time to perform each acrobatic task averaged across five day intervals. There was no significant difference among the intervals.

Figure 6. Mean number of errors made on the rotating rod on each day of testing (learning vs. non-learning). Asterisks indicate that the learning group made significantly less errors than the non-learning group on the first day of testing, $p < .05$.

Figure 7. Mean amount of time to cross the rotating rod on each day of testing (learning vs. non-learning). Asterisks indicate that the non-learning group took significantly more time to cross the rod than the learning group on the first day of testing, $p < .05$.

Figure 8. Mean amount of time to climb the rope on each day of testing (learning vs. non-learning). Asterisks indicate that the non-learning group took significantly more time to cross the rod than the learning group on the first day of testing, $p < .05$.

Figure 9. Mean number of errors made on the rotating rod on each day of testing (immediate vs. delay). Asterisks indicate that the learning group made significantly less errors than the non-learning group on the first day of testing, $p < .05$.

Figure 10. Mean amount of time to climb the rope on each day of testing (immediate vs. delay). Asterisks indicate that the non-learning group took significantly more time to cross the rod than the learning group on the third day of testing, $p < .05$.

Figure 11. Mean amount of time to cross the rotating rod on each day of testing (immediate vs. delay).

Figure 1

Figure 2

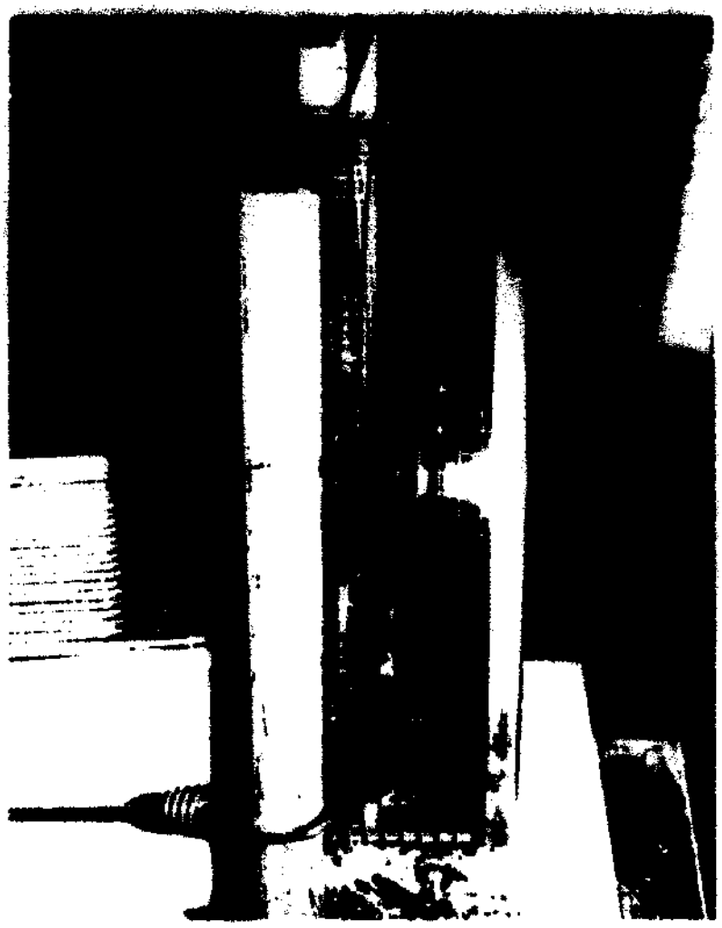
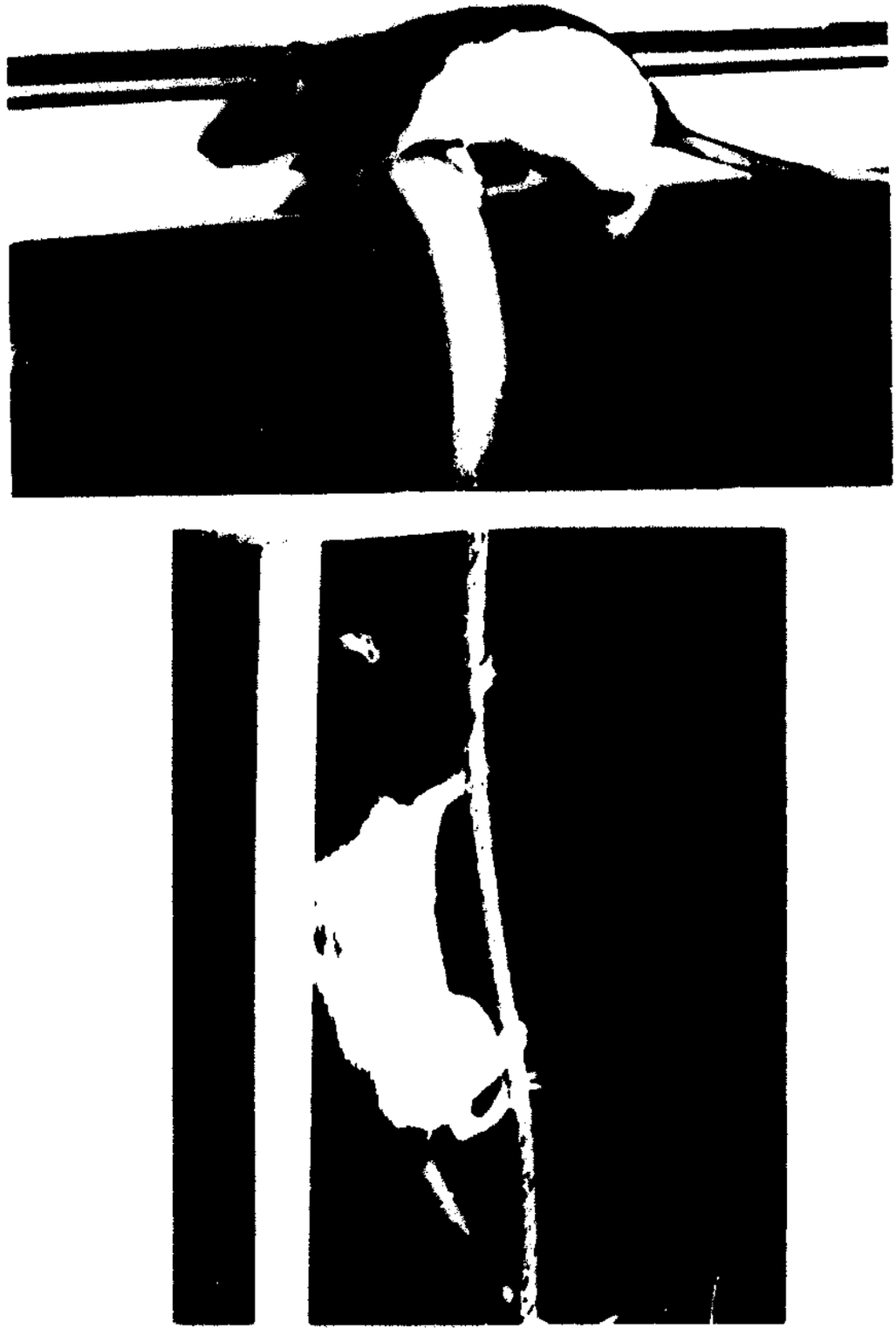


Figure 3



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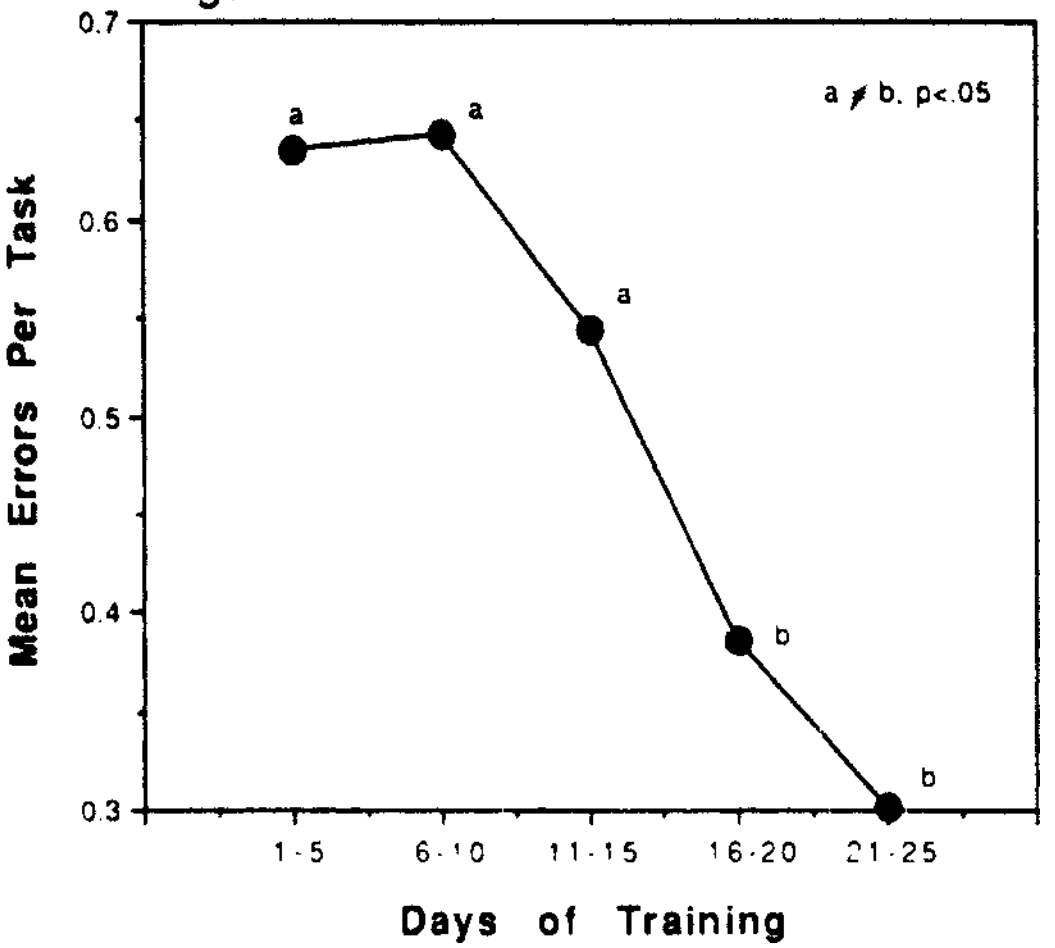

0.7
0.6
0.5
0.4
0.3
Mean Errors Per Task
a ≠ b, p<.05
a
a
a
b
b
1-5
6-10
11-15
16-20
21-25
Days of Training

Figure 5

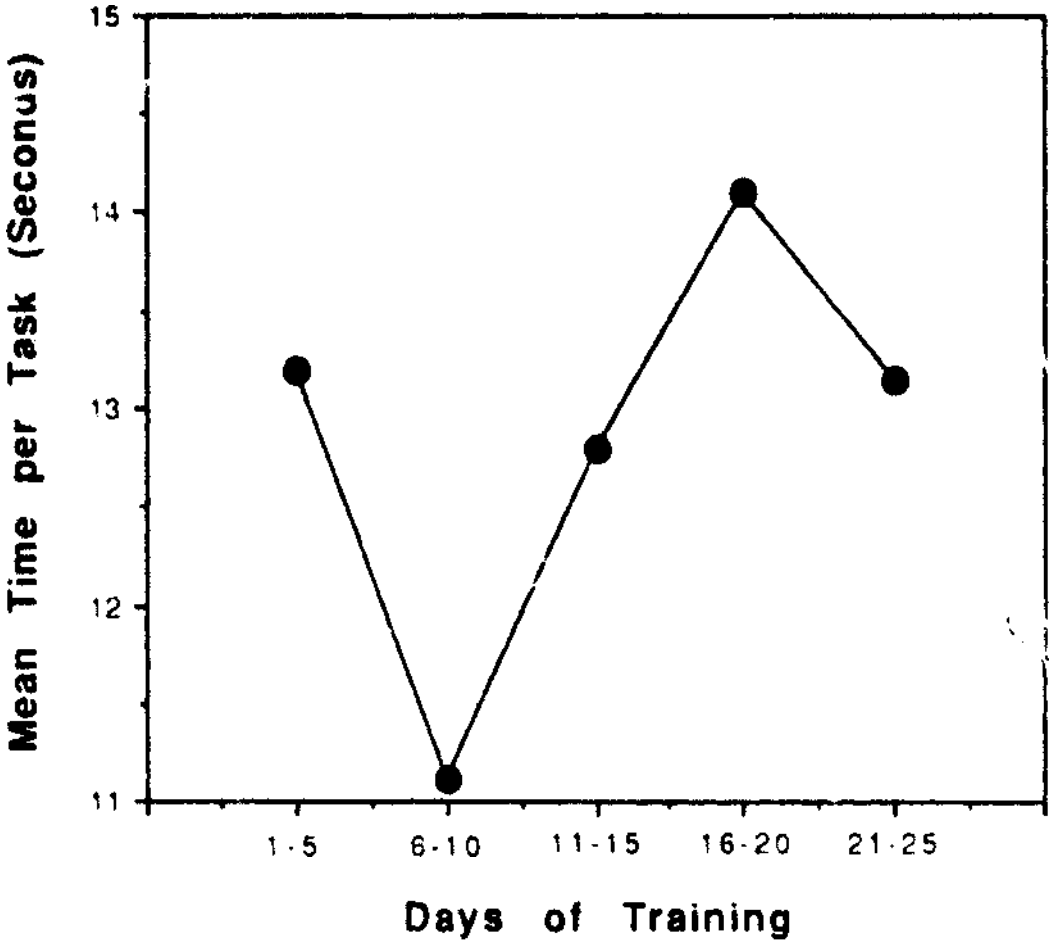

Mean Time per Task (Seconus)
15
14
13
12
11
1-5
6-10
11-15
16-20
21-25
Days of Training

Figure 6

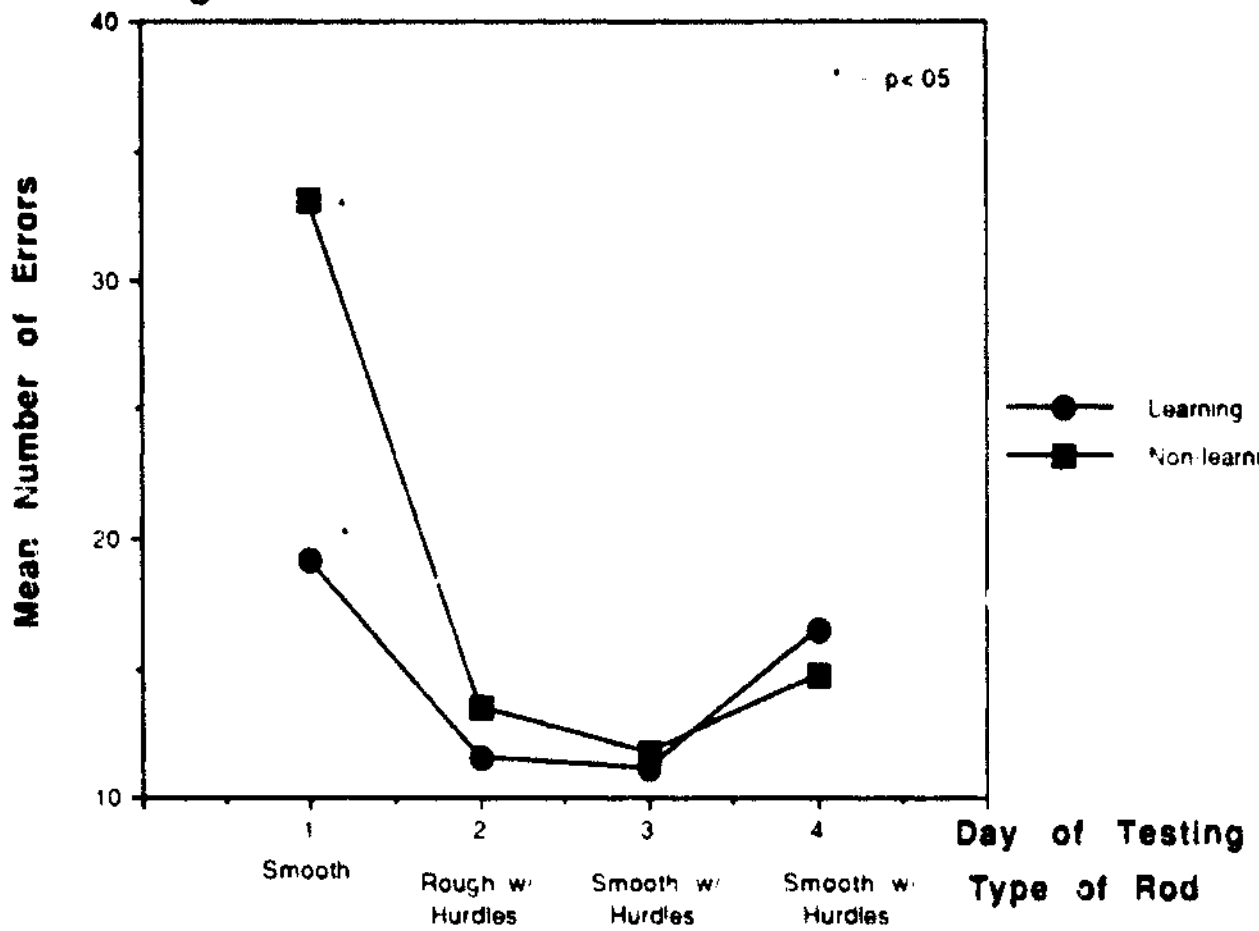

40
30
20
10
* p< 05
Mean Number of Errors
Learning
Non-learning
1
2
3
4
Smooth
Rough w/ Hurdles
Smooth w/ Hurdles
Smooth w/ Hurdles
Day of Testing
Type of Rod

Figure 7

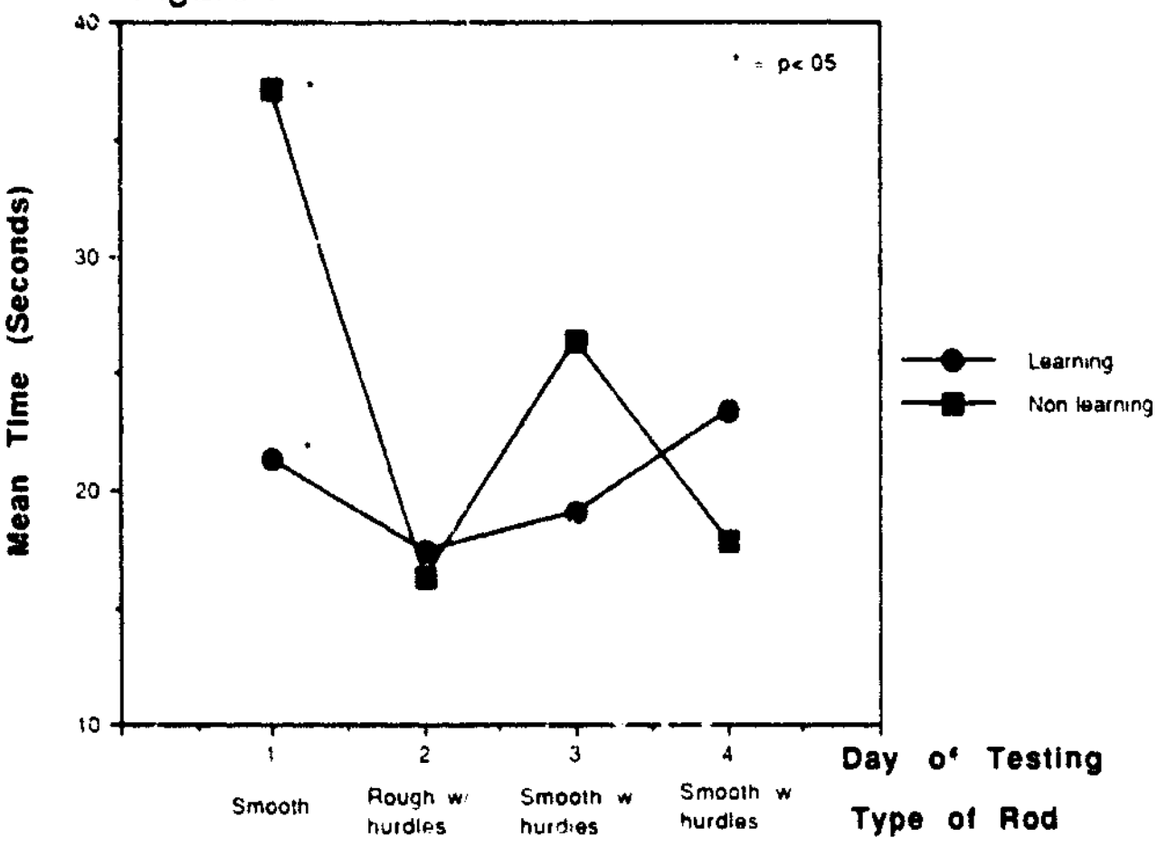

* = p< 05
Mean Time (Seconds)
40
30
20
10
Learning
Non learning
1
2
3
4
Day of Testing
Smooth
Rough w/ hurdles
Smooth w hurdles
Smooth w hurdles
Type of Rod

Figure 8

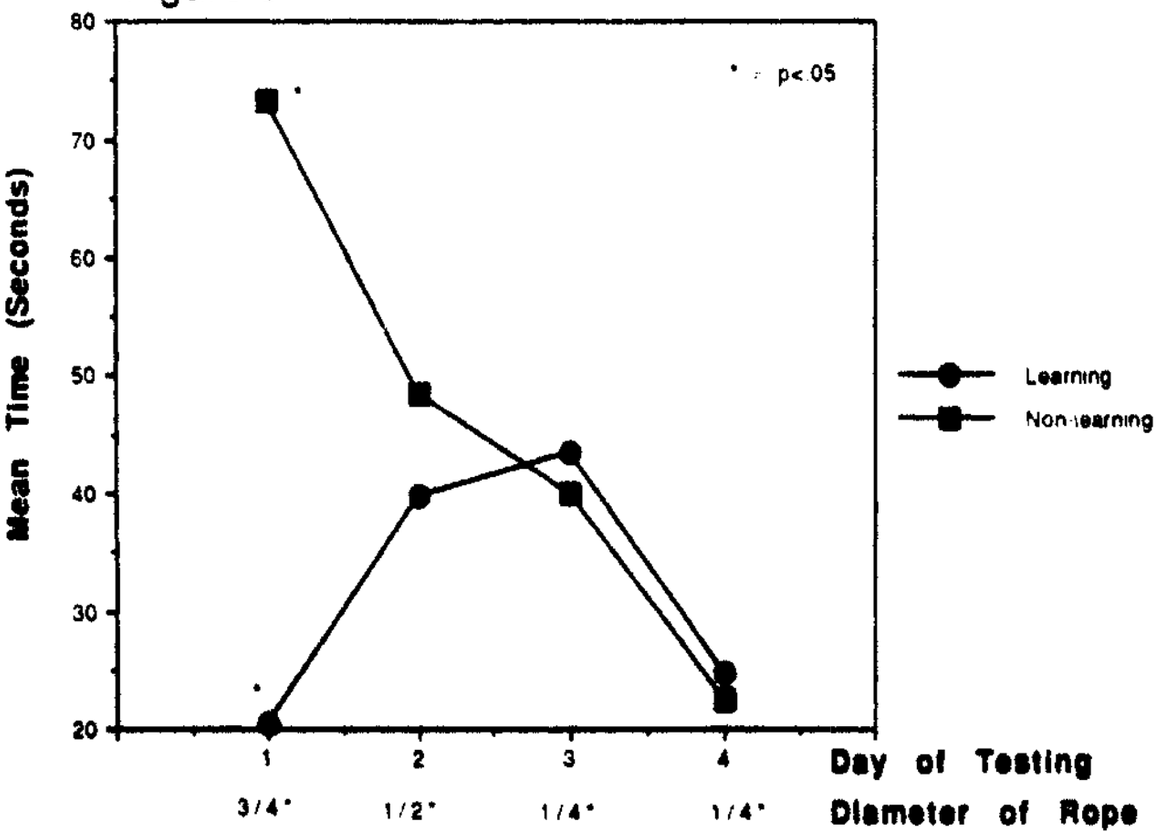

80
70
60
50
40
30
20
Mean Time (Seconds)
* = p<.05
Learning
Non-learning
1
2
3
4
Day of Testing
3/4"
1/2"
1/4"
1/4"
Diameter of Rope

Figure 9

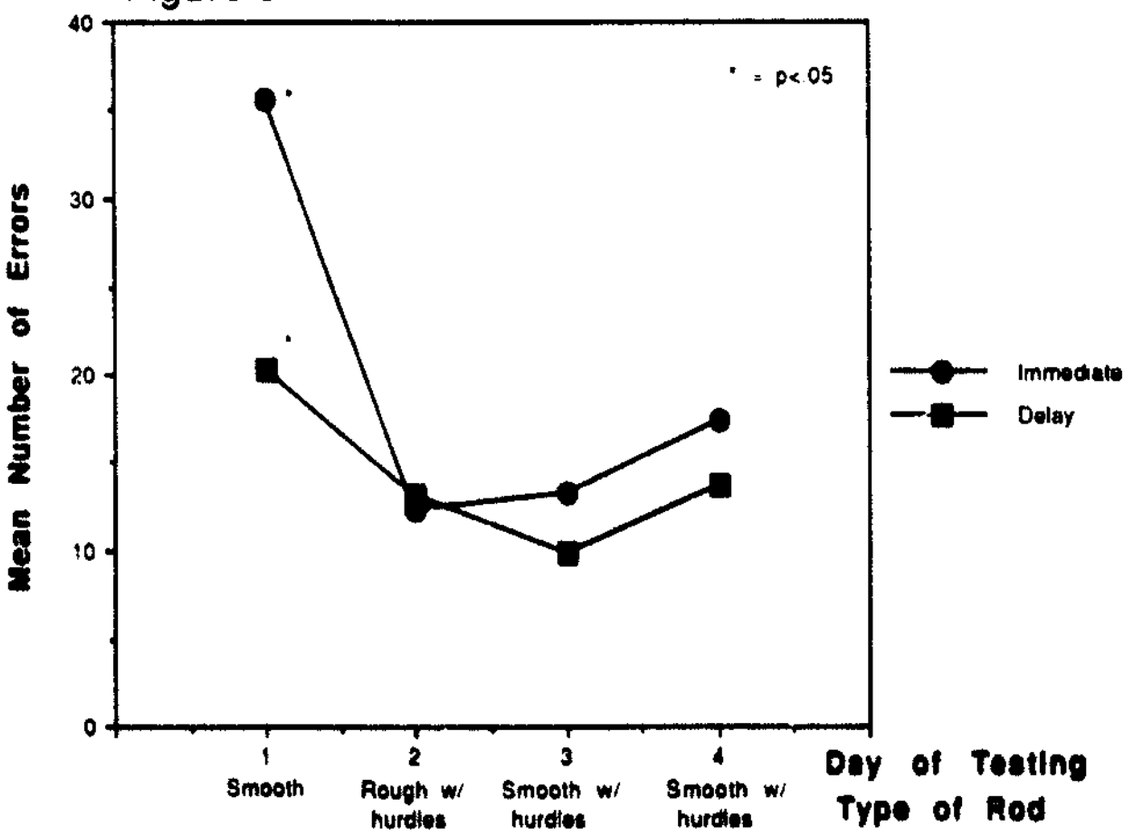

* = p< .05
Mean Number of Errors
40
30
20
10
0
1
Smooth
2
Rough w/ hurdles
3
Smooth w/ hurdles
4
Smooth w/ hurdles
Day of Testing
Type of Rod
Immediate
Delay

Figure 10

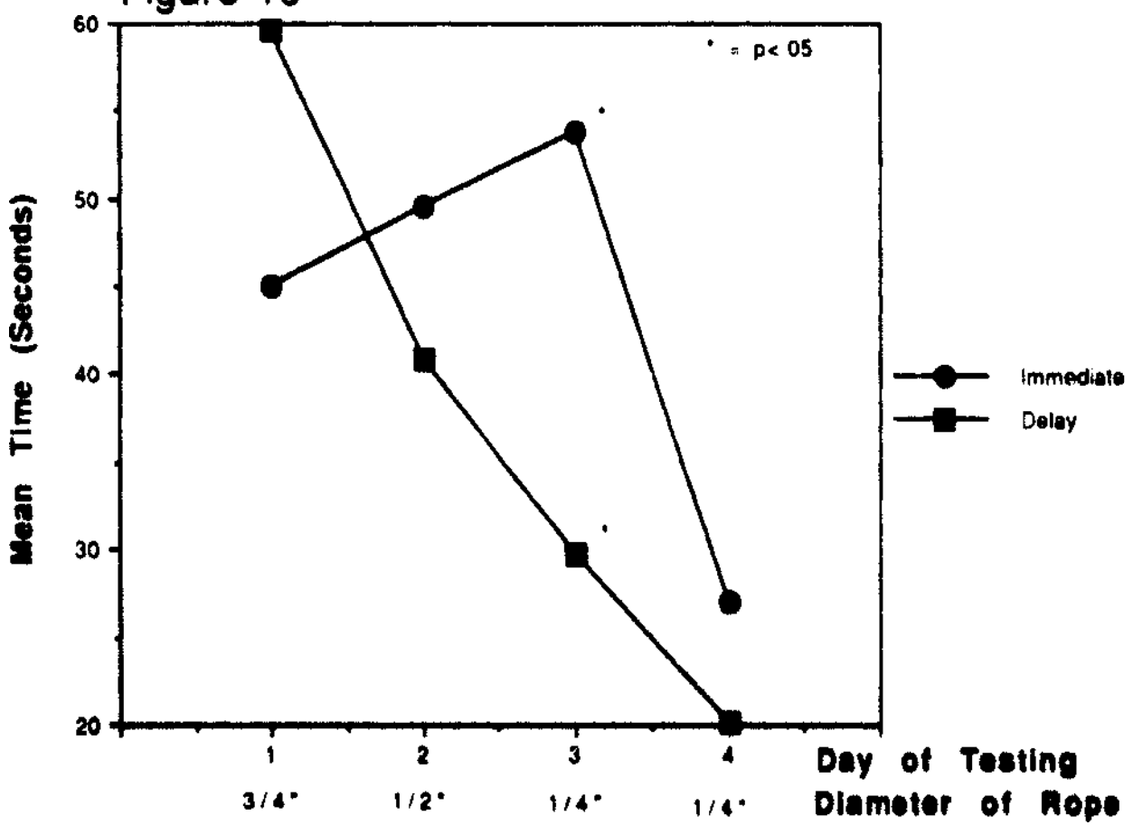
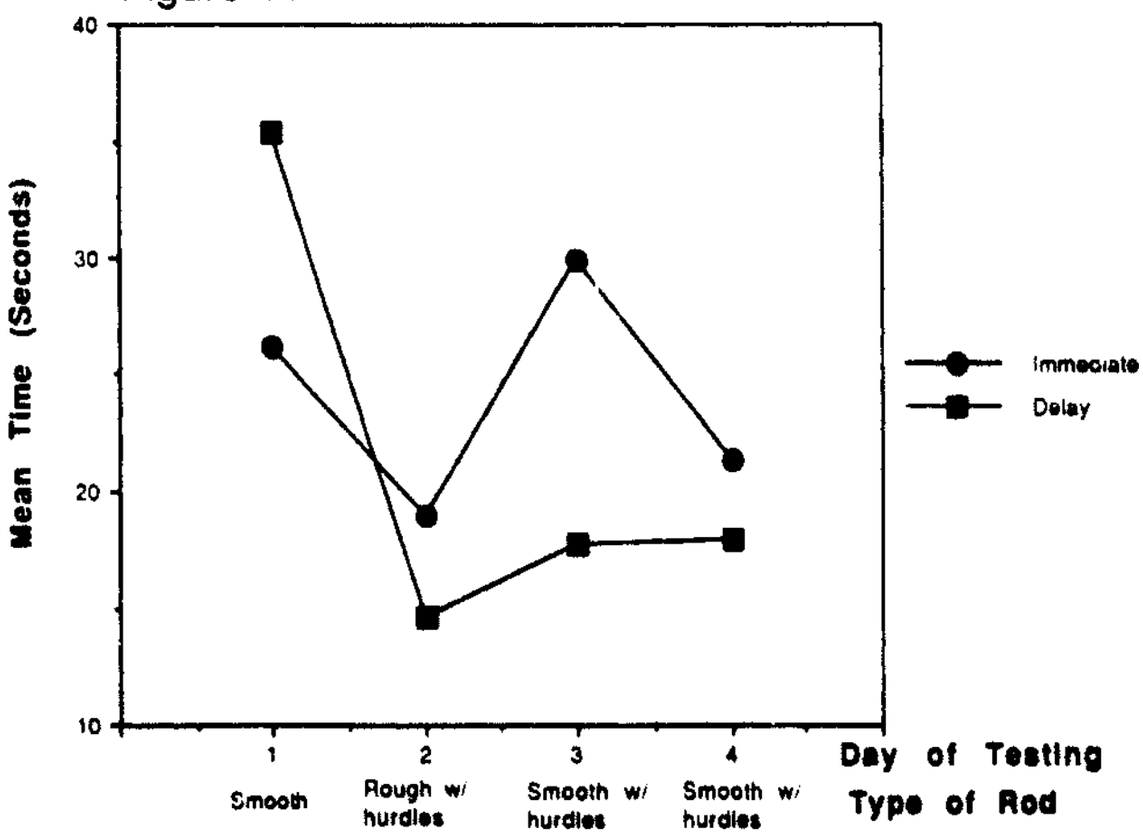

* = p< 05
60
50
40
30
20
Mean Time (Seconds)
1
2
3
4
3/4"
1/2"
1/4"
1/4"
Day of Testing
Diameter of Rope
Immediate
Delay

Figure 11


40
30
20
10
Mean Time (Seconds)
Immediate
Delay
1
2
3
4
Day of Testing
Smooth
Rough w/ hurdles
Smooth w/ hurdles
Smooth w/ hurdles
Type of Rod